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Saurichthys (Pisces, Actinopterygii) teeth from the Lower Triassic of Spitsbergen, with comments on their stable isotope composition ($\delta^{13}C$ and $\delta^{18}O$) and X-ray microtomography

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Abstract: A rich collection of exceptionally preserved Lower Triassic fossil fish remains obtained during the Polish Spitsbergen Expedition of 2005 includes many isolated teeth believed to belong to a saurichthyid actinopterygian. Stable isotope analysis ($\delta^{13}C$ and $\delta^{18}O$) of putative *Saurichthys* teeth from the Hornsund area (South Spitsbergen) acting as a paleoenvironmental proxy has permitted trophic-level reconstruction and comparison with other Lower Triassic fish teeth from the same location. The broader range of $\delta^{13}C$ values obtained for durophagous teeth of the hybodont selachian, *Lissodus*, probably reflects its migratory behaviour and perhaps a greater feeding diversity. X-ray microcomputed tomography (XMT), a non-destructive technique, is used for the first time in order to elucidate details of tooth histology, the results of which suggest that the method has considerable potential as a future analytical tool.

Key words: Arctic, Svalbard, fish teeth, stable isotopes, x-ray microtomography, Lower Triassic.

Introduction

The first saurichthyid actinopterygian teeth and scales from lower Triassic deposits of South Spitsbergen were found during the Norwegian expedition of Hoel and Røvig in 1917 (*vide* Birkenmajer and Jerzmańska 1979), and later described by

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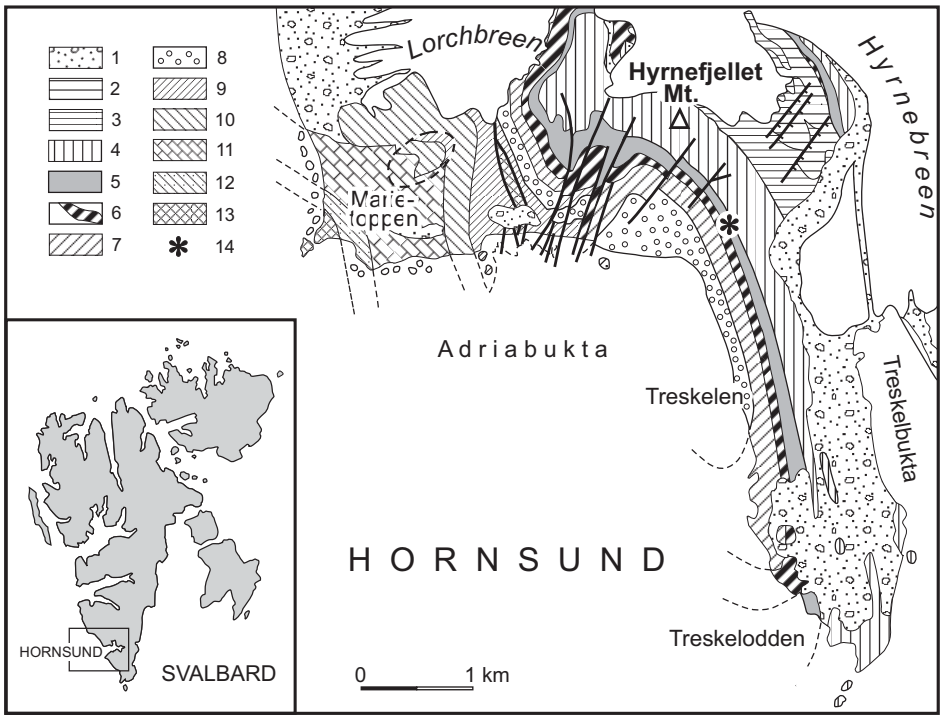

Fig. 1. Geological map of West Spitsbergen, Hornsund area (after Birkenmajer 1964), showing location of the Hyrnefjellet Mt., where the samples were collected. 1 – Moraines, partly outwash; 2 – Festningen Sandstone (Hauterivian–Barremian); Ullaberget Series (Lower Neocomian); 3 – Tirolarpasset Series (Volgian–Lower Neocomian); 4 – Middle and Upper Triassic; 5 – Lower Triassic; 6 – Brachiopod Cherty Limestone (Upper Permian); 7 – Treskelodden Fm (Upper Carboniferous–Lowermost Permian); 8 – Hyrnefjellet Fm (Middle Carboniferous); 9 – Adriabukta Series (Visean–Namurian A?); 10 – Upper Marietoppen Series (Devonian); 11 – Middle Marietoppen Series (Devonian); 12 – Lower Marietoppen Series (Devonian); 13 – Sofiebogen Fm (Eocambrian–Precambrian); 14 – Asterisk shows locality yielding fish teeth.

Stensiö (1921). Based on a detailed study of skeletal fragments from other Triassic localities on Spitsbergen, Stensiö (1925) described four species of the genus *Saurichthys* Agassiz, 1834 (*S. wimani* (Woodward), *S. ornatus* Stensiö, *S. hamiltoni* Stensiö, *S. elongatus* Stensiö). Further fieldwork undertaken to extend the geological survey of Spitsbergen continued with additional participation by Polish scientists. The Polish Spitsbergen Expedition of 1960 (Birkenmajer 1964, p. 14) collected new material from South Spitsbergen, the shark and other fish remains being described by Jerzmańska (in Birkenmajer and Jerzmańska 1979). Later Polish expeditions to the same area included the 2005 visit by B. Błażejowski and A. Gaździcki, who collected samples from the conglomerate of the Lower Triassic Brevassfjellet *Myalina* Bed, cropping out on the southern slope of the Hyrnefjellet Mountain (Fig. 1). Acetic acid treatment of the conglomerate has yielded phosphatic remains including dozens of isolated teeth, mostly of chondrichthyan origin (Birkenmajer and

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Fig. 2. Outcrops of the late Paleozoic–early Mesozoic sequence of Hyrnefjellet Mt., Hornsund. Asterisk shows locality yielding fish teeth.

Jerzmańska 1979; Błażejowski 2004), plus numerous teeth assigned here to *Saurichthys* sp. Although the dentition of *Saurichthys* ("lizard fish") is fairly well known from partial and complete articulated skeletons, isolated teeth are not easily determined to either generic or species level. Several complete or nearly complete skeletons of *Saurichthys* have recently been described from many localities worldwide (Griffith 1962; Duffin and Gaździcki 1977; Mutter *et al*. 2008; Kogan *et al.* 2009; Renesto and Stockar 2009; Wu *et al.* 2009, 2011; Schmid and Sánchez-Villagra 2010; Kogan 2011; Romano *et al.* 2012), representing a considerable advance in our knowledge of the group. *Saurichthys* was a relatively cosmopolitan genus, being so far found in Triassic deposits on every continent except Antarctica.

This paper focuses on isolated *Saurichthys* teeth from the Lower Triassic of Spitsbergen and presents new analyses of their stable isotope composition ($\delta^{13}C$ and $\delta^{18}O$) and structure as revealed by X-ray microtomography.

Geological setting

All the specimens described here come from thin layers of Lower Triassic (Dinerian) fine-grained, iron-rich conglomerate, belonging to the 5–6 m thick

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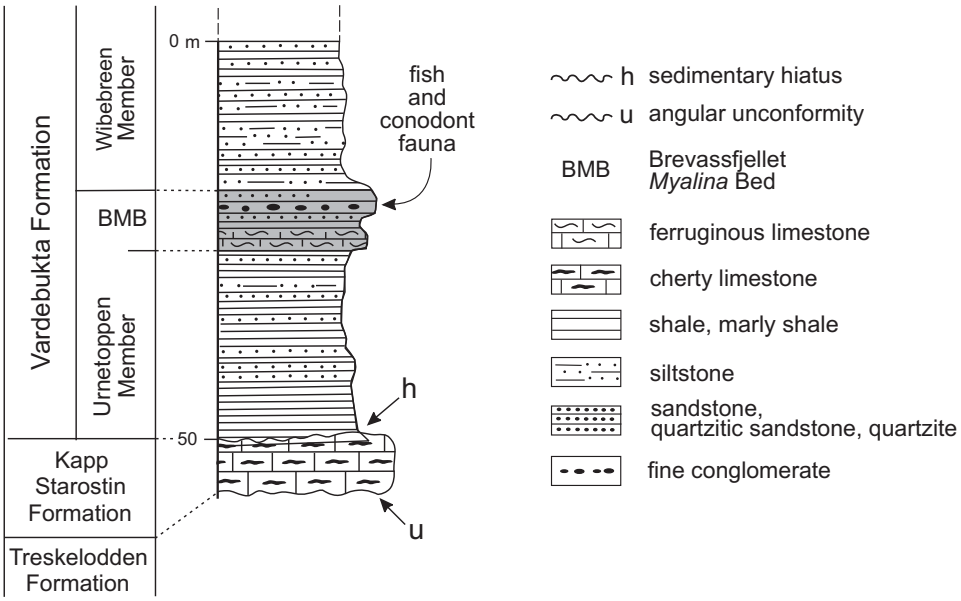

Fig. 3. Position of fish fauna described in the Triassic stratigraphic log of the Hyrnefjellet Mt., Hornsund (after Birkenmajer 1977).

Brevassfjellet *Myalina* Bed (Fig. 3), exposed on the SE slope of Hyrnefjellet Mt. (Figs 1–3) in the Hornsund area of West Spitsbergen. This bed represents the upper part of the Urnetoppen Member of the Vardebukta Formation (Birkenmajer 1964, 1977; Harland 1997; Dallmann *et al*. 1999). The underlaying strata represent Lower Permian rocks, including brachiopod cherty limestone of the Kapp Starostin Fm (Nakrem *et al.* 1992; Dallmann 1999; Nielsen *et al*. 2013) and calcareous clastics of the Treskeloden Fm (Birkenmajer and Fedorowski 1980; Birkenmajer 1984; Błażejowski *et al.* 2006; Błażejowski 2009; Nakrem *et al.* 2009).

The Vardebukta Formation (Buchan *et al*. 1965) is the oldest lithostratigraphic unit of this rank in the Triassic sequence of the Svalbard archipelago (Fig. 3). Both members of the Vardebukta Formation, *viz*. Urnetoppen and Wibebreen, are of marine origin (Birkenmajer and Jerzmańska 1979). The Brevassfjellet *Myalina* Bed is easily distinguished in the field by its intensely brown-red weathering. The rocks abound in organic fragments, mainly bivalves (*Myalina*) and trace fossils. The top of the unit is covered by discontinuous intercalations of quartz conglomerate, 5–10 cm thick. In addition to abundant fish teeth and scales the conglomerate has yielded a few stratigraphically valuable Lower Triassic (Dienerian) conodonts (Birkenmajer and Trammer 1975). The isolated teeth forming the subject of the present study are thus slightly older than the articulated specimens of *Saurichthys* described by Woodward (1912) and Stensiö (1925), which are Smithian in age.

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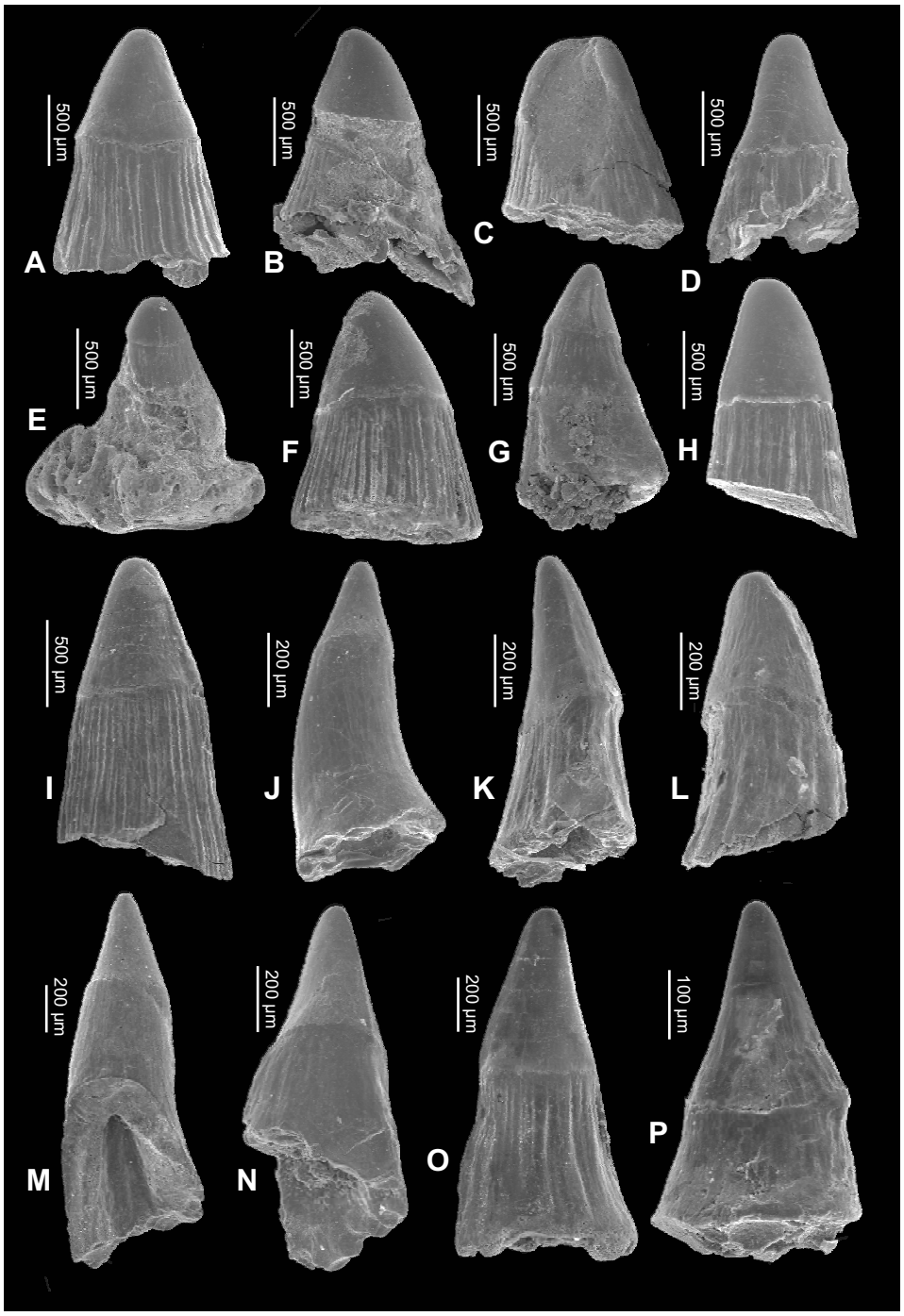

Fig. 4. Teeth of *Saurichthys* sp. Vardebukta Formation, Lower Triassic (Dinerian); Hyrnefjellet Mt., Hornsund.

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Material and methods

The vertebrate material collected by the Paleontological Expedition to Spitsbergen (2005) consists of about 150 isolated ichthyoliths, among them approximately 40 *Saurichthys* teeth (see discussion below; Fig. 4). The fragmentary character of the fish remains suggests reworking by the action of currents. The scales and teeth are often abraded and the roots of the teeth are usually damaged. This shows that the fish-bearing conglomerate is a marine bone bed – a concentrate, which consists of fossil fragments developed by winnowing out the finer clay and sand particles from the sediment by bottom currents, and then deposited as offshore sand bars. The specimens were obtained from the bone bed by dissolving the cement in 10% acetic acid buffered with calcium orthophosphate, then washing, drying, and picking the residue under a binocular microscope.

Illustrated specimens were coated with platinum and photographed using a SEM. Five specimens were analysed for carbon and oxygen isotope composition (Fig. 5) using an automated carbonate reaction device (Kiel IV), which was coupled to a Finnigan Mat Delta Plus mass spectrometer at the Institute of Geological Sciences and the Institute of Palaeobiology, Polish Academy of Sciences in Warsaw. Results are reported in conventional δ notation relative to the VPDB standard (defined via NBS 19). The spectrometer external error is less than ±0.16‰.

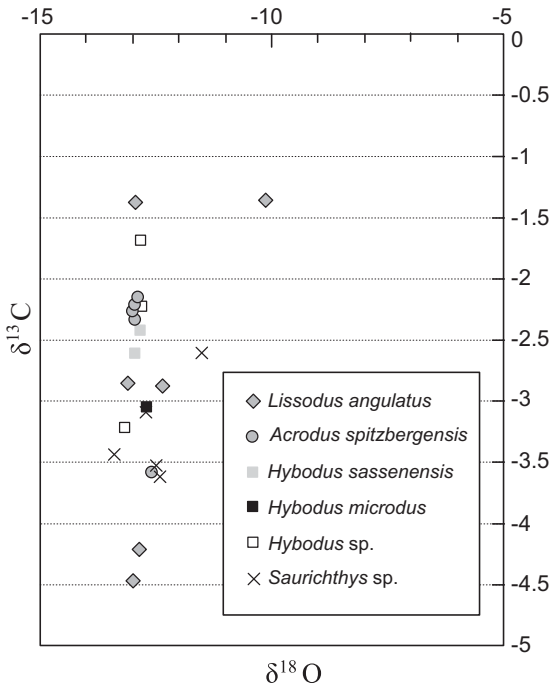

Fig. 5. Oxygen and carbon stable isotopes found in investigated fish teeth.

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Several teeth were the subject of X-ray microtomography measurements using an Xradia MicroXCT scanner which was equipped with a 150 keV sealed tungsten high-energy microfocus X-ray source and a 2048 × 2048 pixel^2 16-bit high resolution cooled CCD detector. X-ray settings included an accelerating voltage of 80 kV and current 125 μA and a lead glass filter was placed just in front of the X-ray source which acted to remove low energy photons from the X-ray beam, thus reducing beam hardening artifacts. 2001 projections were collected over a rotation of 180° using a binning factor of 1 (*i.e.*, the full frame of the CCD). 20× magnification, using a compound objective lens, was used to focus the X-ray image captured by the scintillator screen onto the CCD camera, giving a reconstructed voxel size of 0.6 × 0.6 × 0.6 μm^3. The exposure time per projection was 30 seconds. The projections were reconstructed into 3-D tomographic volumes using a cone-beam extension of the filtered back projection reconstruction algorithm (Feldkamp 1984). The cross-section images were then generated from the reconstruction using professional software (Avizo, VSG, France). The user-dependent threshold has been applied to the whole dataset. The 3D volume and surface renderings (see Figs 6 and 7) after segmentation were performed using the same software and high intensity level methods in the semi-opacity mode.

All figured specimens are deposited in the Institute of Paleobiology, Polish Academy of Sciences, Warszawa (abbreviated ZPAL P.8).

Discussion of the material

The isolated actinopterygian teeth are all fragmentary and their morphological variation is illustrated in Fig. 4. The specimens range in height from 0.8 mm to 1.6 mm. The teeth are all upright; some show a small amount of recurvature (*e.g.*, Fig. 4J) and others possess a slightly sigmoid long axis (*e.g.*, Fig. 4M). Two rough morphotypes can be discerned within the collection: generally larger, robust, rather stubby teeth, each with a comparatively wide base, and generally smaller, more gracile, slender, elongate teeth with a comparatively narrow base. In some specimens, the acrodin cap is blunted by antemortem wear (*e.g.*, Fig. 4C), whereas in others, it is relatively unworn (*e.g.*, Fig. 4N). The cap forms between one third and one half of the preserved height of the tooth, and maybe slightly flattened, possessing lateral cutting edges formed by clearly developed carinae (*e.g.*, Figs. 4G, K–N, 6B$_1$), which may extend past the cap/shaft junction and down the bulk of the length of the shaft (*e.g.*, Fig. 4I). The cap is ornamented by a series of fine, seemingly non-bifurcating longitudinal ridges which ascend toward the cusp apex from the cap/shaft junction (*e.g.*, Fig. 4L). The shaft is rounded to slightly compressed in cross-section (Fig. 4K), and may be slightly flared toward the base (*e.g.*, Fig. 4J, O). It is ornamented over its full length by a series of relatively coarse, non-bifurcating ridges, giving a slightly plicated appearance to the walls of the shaft basally (Fig. 4A, F). The pulp cavity is a third of the

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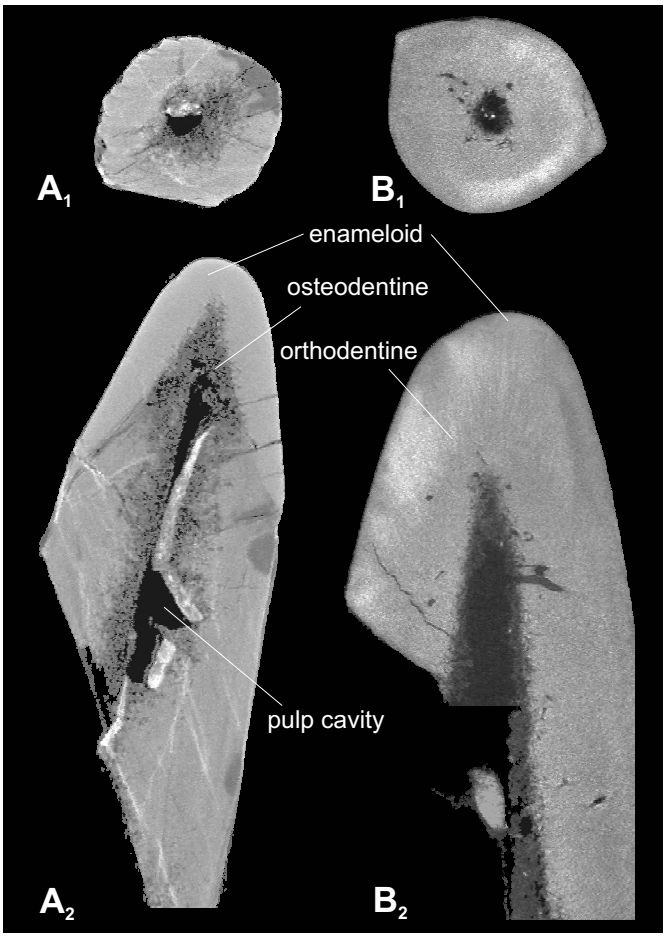

Fig. 6. Transverse (A_1, B_1) and vertical (A_2, B_2) sections of *Saurichthys* sp. teeth from the Vardebukta Formation, Lower Triassic (Dinerian), Hyrnefjellet Mt., Hornsund. **A**. ZPAL P.8/S3. **B**. ZPAL P.8/S18. XMT micrographs.

width of the base, narrowing to around 25% of the diameter of the tooth at the cap, and terminates roughly half way up the cap (Fig. $6A_2$, B_2).

A detailed analysis of the taxonomic position of the teeth used in this study is beyond the scope of the present paper, but some remarks are necessary. The morphology of the teeth described above matches well with those described as *Saurichthys* sp. by Jerzmańska (in Birkenmajer and Jerzmańska 1979), although the specimens at our disposal are rather smaller in size. The genus *Saurichthys* was originally erected on the basis of isolated teeth and fragmentary jaw elements by Agassiz (1833–1843), with *S. apicalis* Agassiz, 1835, based on isolated teeth from the Muschelkalk of Bayreuth, designated the type species. A number of the other species originally erected by Agassiz and included by him in the genus *Saurichthys* have since been removed to other genera; *S. acuminatus* and *S. longidens*,

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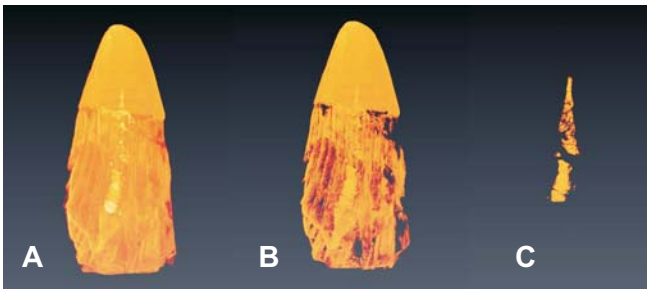

Fig. 7. Tooth of *Saurichthys* sp. **A**. Basic XMT image of tooth, ZPAL P.8/S9. **B**. Visualization of enameloid and collar enameloid with virtually cut out of the internal structure (dentine). **C**. Visualization of pulp cavity. Vardebukta Formation, Lower Triassic (Dinerian); Hyrnefjellet Mt., Hornsund.

for example, have been synonymised and allocated to *Severnichthys acuminata* (Storrs 1994), whilst *S. mougeoti* became the type species of Stensiö's *Birgeria* (Stensiö 1919). All three genera (*Saurichthys*, *Birgeria* and *Severnichthys*) are largely defined on features of the skeleton, patterns of dermal bone sculpture and details of the squamation, with further species being added to both *Saurichthys* and *Birgeria* since their original definition, often with scant attention being paid to dental characters. This illustrates something of the difficulties faced when allocating isolated Triassic teeth to a particular genus. The most comprehensive comparison of the teeth of *Saurichthys* and *Birgeria* remains that of Stensiö (1925, p. 203). He concluded that the teeth of *Saurichthys* could be distinguished from those of *Birgeria* on the basis of (1) the pulp cavity extending, at most, only shortly above the base of the acrodin cap; (2) the base of the shaft is formed of plicidentine; (3) the apical cap is either smooth or ornamented by a series of fine vertical striations, and never develops coarse vertical ridges. These distinctions seem to be confirmed by illustrations and descriptions of the teeth of these two genera in subsequent publications (*e.g*., Gardiner 1960; Schwarz 1970; Griffith 1978; Rieppel 1985, 1992; Bürgin and Furrer 1992, 1993; Mutter *et al*. 2008). Bürgin and Furrer (1993) discussed Stensiö's character list in relation to a large actinopterygian jaw element from the Upper Triassic of Graubünden (eastern Switzerland), tabulating a useful summary of relevant features (Bürgin and Furrer 1993, p. 1027). Bearing the foregoing discussion in mind, the Spitsbergen teeth described and studied here are best accommodated in the genus *Saurichthys*, displaying only fine ornamentation on the apical cap and simple plication of the shaft basally. The penetration of the pulp cavity to a position above the base of the apical cap (see below) may be a variable feature, or might suggest that a second, possibly non-saurichthyid taxon with similar morphology is represented in the sample.

The body form of *Saurichthys*, as clearly demonstrated from articulated specimens collected and described from a wide range of Triassic localities, suggests that it is a pelagic fish, feeding as an ambush predator (Rieppel 1992; Lombardo and Tintori 2005).

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Carbon and oxygen stable isotope composition as an environmental proxy

Analysis of the isotope compositions of biogenic minerals has much potential as a palaeoecological tool; it is known that isotope compositions depend on aspects of the original habitat of the animal (water temperature, depth, and chemical composition), its diet (and therefore trophic position) as well as subsequent geological processes such as diagenesis. Since the latter process can cause overprinting of the original biogenic isotopic signals, enamel, which is very resistant to isotopic exchange, is the most commonly sampled tissue.

Kolodny *et al.* (1983) and Vennemann *et al.* (2001) have described the application of biogenic phosphates to palaeoenvironmental studies, but the approach was limited by analytical difficulties associated with using phosphatic material. Because of this, our palaeoenvironmental reconstructions to date have relied on analyses of biogenic carbonates.

Carbon and oxygen stable isotope compositions for some *Saurichthys* teeth were compared with those obtained from the teeth of five species of hybodont shark

Table 1

Isotope data of the measured Lower Triassic fish teeth from Spitsbergen.

Sample	Samp. ID	$\delta^{18}O$	$\delta^{13}C$
Lissodus angulatus	BBR2	-12.356	-2.877
Lissodus angulatus	BBR6	-12.863	-4.213
Lissodus angulatus	BBH18	-13.11	-2.858
Lissodus angulatus	BBH19	-12.951	-1.371
Lissodus angulatus	RBB 31	-10.148	-1.359
Lissodus angulatus	RBB 32	-13.003	-4.469
Acrodus spitzbergensis	BBR3	-12.955	-2.27
Acrodus spitzbergensis	BBR7	-12.588	-3.581
Acrodus spitzbergensis	BBH13	-12.946	-2.336
Acrodus spitzbergensis	BBH14	-12.916	-2.208
Acrodus spitzbergensis	RBB 36	-12.894	-2.16
Hybodus sassenensis	RBB 34	-12.837	-2.43
Hybodus sassenensis	RBB 35	-12.93	-2.618
Hybodus microdus	BBR5	-12.698	-3.051
Hybodus sp.	BBR4	-12.802	-2.231
Hybodus sp.	BBR8	-12.833	-1.684
Hybodus sp.	BBH16	-13.148	-3.216
Saurichthys sp.	BBR1	-11.524	-2.599
Saurichthys sp.	BBH11	-12.504	-3.522
Saurichthys sp.	BBH12	-12.733	-3.098
Saurichthys sp.	RBB 37	-12.42	-3.616
Saurichthys sp.	RBB 38	-13.403	-3.441

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(*Lissodus angulatus* (Stensiö, 1921); *Acrodus spitzbergensis* Hulke, 1873; *Hybodus microdus* Stensiö, 1921; *Hybodus sasseniensis* Stensiö, 1918 and *Hybodus* sp.) collected from the same Brevassfjellet *Myalina* Bed (see Table 1; Fig. 5). Each set of fossilised teeth has been analysed in an attempt to determine the influence of habitat, diet, and possible species-specific fractionation effects on the isotopic composition of biogenic carbonates in fish. With the exception of *Saurichthys* and *Lissodus* (Błażejowski 2004) all of the teeth which have been investigated exhibit $\delta^{18}O$ values within the narrow range of 0.9‰ (oscillating around -12.7‰ VPDB). Such small differences suggest that the hybodonts *Acrodus* and *Hybodus* lived in approximately the same environment, presumably within waters of identical mean composition. In this context, the small hybodont *Lissodus*, a durophagous bottom-dwelling shark, seems to be a migratory species, appearing from time to time in the habitat occupied by the other fish genera. The palaeoecology of this taxon is controversial and is the subject of recent debate. Several reports have been published reconstructing the palaeoecology of *Lissodus* from late Triassic Central European Basin using oxygen isotopes (Fischer *et al.* 2009, 2010, 2012). Results of isotope composition analysis reported in Fischer *et al.* (2012) show values of $\delta^{18}O$ less than 15‰ VSMOW. This is interpreted as being due to a brackish water influence, but such low values might also indicate some degree of diagenetic alteration. The results presented in our study are very similar in the context of paleoevironmental interpretations, although expressed in relation to the PDB standard. It should be noted that the paleotemperature equation used in Fischer *et al*. (2012) seems not to be accurate due to differences in $\delta^{18}O$ analytical standards. For details see Puceat *et al.* (2010), especially their remarks in the introductory section of the paper.

The conclusions of this study state that teeth of *Lissodus* indicate life in a non-marine (brackish) environment and behaviour without substantial habitat migration. *Saurichthys*, like other small fish, might be more active than sharks and occur over a wider depth range.

The $\delta^{13}C$ values for complete teeth (dentine plus enameloid) range from -1.3 to -4.4‰ for all the examined fishes, and may reflect differences in diet amongst different fish groups (Fig. 5). Considering the values obtained for *Lissodus*, and its suggested migratory behavior, perhaps it was the most opportunistic (non-selective) feeder amongst the species sampled in this way. Conversely, the more restricted range of the $\delta^{13}C$ values for *Saurichthys* teeth (varying from -2.5 to -3.6‰) suggests that *Saurichthys* may have had a less diverse diet. We are not aware of any direct evidence for dietary components in *Saurichthys* (*e.g.,* confidently assigned coprolitic material or gastric residues in articulated specimens), but the nature of the dentition suggests that it might have fed on smaller fish.

Trophic level reconstructions using this type of data from fish teeth has much interest and potential for broad applications in future studies, especially if combined with parallel studies on modern food chains. Research on chemical and isotopic composition of phosphates from teeth, utilising the most recent analytical

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tools and techniques, should be considered as a powerful and potentially promising palaeoenvironmental proxy.

X-ray microtomography

Traditionally, sectioning is one of the most commonly used methods for investigation of the histology of fossil fish teeth (*e.g.*, Rees and Underwood 2002; Błażejowski 2004; Wang *et al.* 2007; Sasagawa *et al.* 2009). This technique destroys the specimens under investigation, is a time-consuming process, and may be technically demanding in the case of small specimens. Certain teeth, when immersed in aniseed oil, can be studied by normal light microscopy, revealing details of their histology (see Duffin and Ivanov 2008). As far as we are aware, X-ray microcomputed tomography (XMT) has not been applied in studies of fossil fish teeth, although it has been successfully used for recognition of soft-tissue preservation in invertebrate fossils (*e.g.*, Sutton 2008; Błażejowski *et al.* 2011; Zapalski and Dohnalik 2013) and for studies of fossil vertebrates (*e.g.*, Kin *et al.* 2012; Nowaczewska *et al.* 2013).

The primary aim of the current study is to test the application of XMT as a non-invasive tool for detailed histological imaging of tiny fossil fish teeth. The purpose for using high resolution scanning was to bring new light into fish taxonomy based on very detailed images of the histology. XMT allows quantitative and qualitative analysis of dental tissues (enameloid, collar enameloid and dentine), and with the possibility of 3-D reconstruction and modelling, enables investigation into morphological variation as well as making precise measurements for morphometric studies.

Typical enameloid is usually found at the tip of the tooth in actinopterygian, and is called cap enameloid or the "acrodin cap" (Wang *et al.* 2007). The term collar enameloid is applied to the majority of collar tissue that covers the surface of the tooth shaft (Fig. 6) (Shellis and Miles 1974). Collar enameloid is basically homologous with cap enameloid, but differs in its structure (Sasagawa and Ishiyama 1988). Both tissues are undoubtedly generated differently in different groups of actinopterygians.

The XMT technique, which relies on the differential attenuation of the X-ray beam propagating through objects of different densities, was used to produce a 3-D model of collar enameloid and pulp cavity histology (Figs 6 and 7). Background was removed from the images by thresholding, and virtual cross-sections in axial (Fig. $6A_2$ and B_2) and transversal planes (Fig. $6A_1$ and B_1) were generated. Further cross-sections can be computed in any desired plane based on entirely the same data. The high resolution images obtained by this technique revealed subtle details of the histology and, with aid of 3-D reconstructions, has much potential as a taxonomic tool for future studies.

The small collection of actinopterygian fish teeth from Brevassfjellet *Myalina* Bed described by Jerzmańska (Birkenmajer and Jerzmańska 1979) was left in open

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nomenclature. She proposed, however, assigning different morphotypes to three separate species.

Our study of two teeth with very similar morphology using microtomography reveals significant differences in inner structure which might have taxonomic implications. Specimen A (Fig. 6A) has internal tissue (dentine) formed as "osteodentine" with a clearly defined pulp cavity in the central part. Specimen B (Fig. 6B) has "ortho-dentine", with no pulp cavity visible, but with the central tissue similar to osteodentine. Taking this into account, it may be that the microstructure of *Saurichthys* teeth indicates the coexistence of two types of histology within a single taxon, as in some hybodont sharks (Błażejowski 2004). However, the organic matrix formed in the enameloid and collar enameloid during the matrix formation stage may also differ. This suggestion requires more detailed studies on further samples for verification. Another possibility is that two separate taxa may be represented by the two specimens, in spite of their close morphological similarity.

It should be noted that the use of XMT coupled with virtual imaging reconstructions permits detailed investigation of very small specimens, with the potential of elucidating features of taxonomic significance that are not visible if morphology alone is considered. The technique has the advantage that, being non-destructive, it can be applied to valuable and unique specimens, and the maximum size of the object under investigation is limited only by the equipment used.

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